

LETTER TO THE EDITOR

Further Comments on Variation in Vireo

I would like to take this opportunity to clarify certain misunderstandings which, as A. L. Rand (1961. *Wilson Bull.*, 73: 46-56) points out, seem to have resulted from my paper on "Adaptive variation in the genus *Vireo*" (1958. *Wilson Bull.*, 70: 307-346).

(1) In my paper, I was attempting to show that the effects of selection pressures for large size in the cooler parts of the ranges of species are frequently masked in other regions by additional selection pressures superimposed on the operation of the effect of low temperature. Taking Bergmann's rule for granted, I concentrated on additional factors which conceivably might effect geographical variation in body size and wing length. To make sure that this would not be misunderstood, I introduced my paper with these sentences (1958: 308): "Before continuing, I would like to point out that my conclusions, reported in this paper, on the adaptive significance of variation in body size within the species of *Vireo* and some other New World species *do not invalidate* Bergmann's rule. Rather, I interpret my findings to represent alternate possibilities: First, other selective forces . . . may mask, modify, or interact with the selective action of cold temperature . . ." (Rand, incidentally, does not question my use of the theory of combined operation of additional selective factors; this is evident from the similarity between my comments quoted here and the concluding sentence to his paper (1961: 55), "More than one factor could be in operation at one time, working in different directions, canceling, or modifying each other.") Then, after citing some trends for intraspecific increase in wing length in the Sonoran region, I wrote (1958: 324) that "Finally, I find little evidence for the presence of Bergmann's rule, *per se*, within New World species." This sentence is ambiguous, open to misunderstanding, and seemingly in conflict with my comments elsewhere in the paper. The *per se* referred to the operation of Bergmann's rule without evidence of superimposed, additional selection pressures, and, thus, I feel that Rand is less than precise when he reports (1961: 46) my findings in the words "Hamilton, in 1958, writes that he can find little evidence for the application of Bergmann's rule (wing length and presumably body size being greater in colder climates) within New World species."

The few examples of larger wings and body weights in North American regions of low environmental temperatures, which Rand has listed, do not come to grips with the issue I raised in my paper, namely, that of the possible operation of additional selection pressures on wing length and body size in the southwestern region of North America. Nor do conclusions (Rand, 1961: 54) based on comparisons of the wing lengths and weights of populations from eastern and western United States provide a test for the validity of the aridity effect.

(2) Discussing the aridity effect, Rand states (1961: 54) that "On the basis of longer wing length of populations from the western part of North America, [Hamilton] postulated a greater body weight . . ." I find the first part of this quote puzzling since the aridity effect, as I formulated it, is a speculation (1958: 323) derived from intraspecific increase of wing length in *southwestern North America* (Sonoran region)—made clear by my comparison of these large winged Sonoran populations with conspecific populations from more northerly portions of western North America. A comparison of populations from eastern and western United States appears irrelevant to a critical analysis of the above problem. I present the following comments in complete agreement with Rand's statement (1961: 47), about equating wing length with weight, that "If accepted for

samples of birds of the same species from distant areas with widely different environments, there is danger of falling into grievous error."

To disprove the aridity effect, one would first have to demonstrate that such a tendency for intraspecific increase in wing length *and* body weight in the Sonoran region does not exist. Rand writes (1961: 54) "But, [Hamilton] had no weights." I had planned to delay further in reporting (manuscript in preparation) on the matter until I had adequate material to test the point in several species. The limited data available for *V. solitarius*, however, do support the postulated trend for Mexican increase in size (i.e., if we assume that body weight is a valid indicator of size). For example, consider the variation in three western races of *V. solitarius*: *cassinii*, *pinicolus*, and *repetens*. The distribution of these three breeding segments are, respectively and approximately, western United States, Sonoran Mexico, and southwestern Mexico. For males of the first race, Rand lists (1961: 51) values of 72 mm. and 15 grams; for the second race, there are available nine male specimens (Museum of Vertebrate Zoology: collected during June–July, 1957–1959, in the Sierra del Nido, Chihuahua) with average values of 82.7 mm. (81–85) and 18.0 grams (16.3–20.7); and, for the third race, two male specimens (Texas Cooperative Wildlife Collection) have August values of 81 mm. and 17.2 grams and 81 mm. and 19.2 grams.

How valid an indication of size body weight is, is still uncertain, and when more information about the variation in *V. solitarius* is available, my analysis of the variation may well be superseded. Any explanation, for the present, is hypothetical. For example, one might argue that populations of this species in Sonoran Mexico have longer wings and greater weights resulting from the operation of Bergmann's rule because of occupation of habitats in cooler, montane regions, but, then, this may not be the complete explanation since these populations appear to move south during the winter. One might also argue that populations of the *pinicolus* segment have increased wing lengths as a result of utilization of more open habitats, but, then, their body weights seem also greater than those of conspecific populations to the north in, say, Nevada, or to the northeast in eastern United States (see data for this species cited by Rand, 1961: 51). Finally, one could argue that populations of the *pinicolus* segment appear to have greater wing lengths, simply because the *cassinii* populations have smaller wing lengths in association with reduced body size as an auxiliary adaptation facilitating long-distance migration (for a discussion of such possibilities, see Hamilton, 1961, *Evolution*, 15: *in press*). However, this may not be the complete explanation since the *pinicolus* segment appears to consist of migratory populations which winter farther south in Mexico, where, apparently, occur resident populations of the *repetens* segment. In the light of such considerations, the aridity effect can only remain as previously presented—i.e., a speculation.

(3) Rand writes (1961: 52) that I state "that *Vireo olivaceus* and *V. griseus* show the tendency for insular populations to have 'greater wing length and relatively longer bill length (see Murphy, 1938).' " In reality, I stated (1958: 334) that "The strongly isolated, insular representatives of the Caribbean area show the tendency for insular populations to have greater wing lengths and relatively longer bill lengths (see Murphy, 1938)." The Murphy reference, as Dr. Rand states correctly, refers only to variation in bill length, and I regret not having made it clear that the citation in parenthesis refers only to the immediately preceding item (bill length).

I should like to add that for several years I have believed (without giving the matter much thought one way or the other) in the following theory: that there exists in some groups a tendency for insular populations derived from continents, or for populations of small islands derived from large islands, to acquire slightly greater wing lengths

(indicating, presumably, increases in size). For example, if one examines the data for variation in the superspecies *V. olivaceus* and *V. griseus* (Hamilton, 1958: 317, 325), it appears that the Caribbean populations tend to exhibit approximately equal or greater wing lengths than their superspecific counterparts on the adjacent American mainland. (The way Rand (1961: 52) lists my data for these two species prevents observation of this point.) Using my data for these two species, of the values (to the nearest 1.0 mm.) for the 12 Caribbean populations, five are larger, six are intermediate or equal, and one is smaller, when superspecific comparisons are made to the values and ranges of values for the American mainland, lowland populations (from Panama to Florida). The tendency among the vireos of the Caribbean islands to have increased wing length is, to me, unmistakable, provided one makes the comparison with adjacent mainland populations, from which the Caribbean ones are apparently derived.

It would be a good thing if others would take up the problem of the influence of insularity on wing length and size. Mayr and Vaurie (1948. *Evolution*, 2: 253-255, 260) have noted some evidence in the Dicuridae for a tendency of populations or isolates of small islands (12 of 17 cases for *Dicurus leucophaeus* and *D. hottentottus*) to have greater wing lengths than conspecific populations of adjacent, larger islands. Among the passerine races endemic to Cozumel Island off Quintana Roo (see data of R. A. Paynter, Jr., 1955. The *Ornithogeography of the Yucatán Peninsula*), four seem larger (*Troglodytes musculus beani*, *Dumetella glabrirostris cozumelana*, *Cyclarhis gujanensis insularis*, and *Richmondia cardinalis saturata*), five are equal, and two appear smaller, when size comparisons are made to conspecific races on the adjacent mainland. However, absences of such a tendency can also be cited. Lack's data (1947. *Darwin's Finches*) for members of the Geospizidae, when arranged according to size of islands, seem not to show the tendency.

Discussing my data for populations of *Vireo* having breeding distributions in the Caribbean, Rand assumes (1961: 52) that the insular variation is due to "irregularity." He thus believes that my data do not demonstrate a "regularity," even though I reported only about "the tendency." While there can be no doubt that "irregularity" in some way is a component of character variation for any population or isolate, I am not willing to consider this as the only explanation for the variation in wing length of Caribbean vireos. My present stand on the matter (and I have no quantitative evidence for this) is that when continental populations reach small islands, a variety of centripetal selection pressures for specific niche or climatic adaptations may be relaxed, thereby permitting in time more general adaptations to be favored, involving, in some cases, increases in size. However, stringent competition can occur in the depleted or uniform habitats of small islands, and my comments refer mostly to pioneering populations exploiting previously vacant ecological niches and habitats.

(4) In conclusion, when I wrote my 1958 paper, I presented data in an attempt to unify the theories for ecogeographic variation in wing length and size in birds. That attempt leaves, admittedly, much to be desired, as does my current attempt (1961. *Evolution*, 15: *in press*). For example, the evidence for the aridity effect is still sparse and equivocal, and the evidence for the warm-humidity effect (*op. cit.*) can always be explained away as indicating an absence or reduction in operation of Bergmann's rule. The principal object of these two papers was to stimulate the collecting of new data and to propose new working models and alternate explanations, but not to disprove the work of others.—TERRELL H. HAMILTON. *Harvard Biological Laboratories, 16 Divinity Avenue, Cambridge 38, Massachusetts, 20 April 1961.*